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ABSTRACT

We captured 96 individual Swainson's Thrushes (Catharus ustulatus swainsoni) *in 3 habitat types during 6 annual netting sessions at Reserva Las Tangaras in western Ecuador. Capture rates were highest in an Ecotone Habitat of abandoned pasture bordered by remnant tropical montane forest (TMF) along drainages, intermediate in Riparian Secondary Growth TMF, and lowest in Mature Upland TMF. We recovered six individuals at least one year following initial capture: two males, one female, and three of unknown sex. Five were first caught as Hatching Year birds and one as an After Hatching Year bird. All recoveries occurred in or near the net of first capture. One male had migrated round-trip to Ecuador 5.5 times. Swainson's Thrushes were netted most often near streams and drainages independent of forest maturity and fragmentation, suggesting that clearing riparian vegetation for cattle grazing or recreation could harm thrushes on their wintering grounds. Geo-locators might be employed on wintering thrushes to determine their stopover and breeding sites.*

INTRODUCTION

Documenting wintering areas and winter habitat preferences of Nearctic-Neotropical migratory birds contributes to basic biology and avian conservation (Phillips 2018). Far less is known about Neotropical migrants on their Central and South American wintering grounds than on North American breeding grounds (Webster and Marra 2005, Faaborg et al. 2010). *Catharus* thrushes are ideal for studies of migratory passerines because they are relatively common, easily monitored with mist nets, and are large enough to carry tracking devices (Bowlin et al. 2005, Delmore et al. 2012).

The Swainson's Thrush (*Catharus ustulatus*) species has a russet-backed subspecies (*C. u. ustulatus*) that breeds on the Pacific Coast and winters in Central America and an olive-backed subspecies (*C. u. swainsoni*) that breeds in continental forests of the interior and northeastern coast of North America and winters in South America (Ruegg 2007, Phillips 2018). Here we report on the site fidelity and habitat preferences of individuals of the olive-backed subspecies at a wintering site in Andean tropical montane forests (TMF) of western Ecuador.

METHODS

Since 2004, Becker has monitored birds in a ~50-hectare study area composed of TMF in three stages of succession on and adjacent to Reserva Las Tangaras (Figure 1.). Approximately 25 ha of the study area lie within the reserve at elevations ranging from 1300 meters to 1540 m. This portion of the study area consists of two habitat types: ~50% Mature Upland TMF and ~50% Riparian Secondary Growth TMF in areas close to the Nambillo River and its tributaries. The Riparian Secondary Growth TMF has been regenerating from pasture for 25 years and only a few small clearings less than 1 hectare remain around the reserve research cabin.

At the start of monitoring in 2004, the hillside facing the reserve to the north (on the other side of the Nambillo River) had ~60% of the land cleared as pasture and ~40% as remnant TMF. The remnant TMF had been left in strips up to 60 m wide to protect small ephemeral drainages from eroding the hillsides and as patches on slopes

too steep for grazing forming a close association between the remnant TMF and water features. In 2011, cattle were removed from the pastures in the study area and the pasture was abandoned. By 2013, shrubby secondary growth replaced most of the grassy pastures and secondary forest was expanding outward from the remnant TMF along the drainages, forming our third habitat type: an Ecotone Habitat between the abandoned pastures and remnant TMF (Figure 1).

Annual mist-netting in each of the three habitat types began in 2013 to monitor both Neotropical migrants and residents and compare their habitat affinities. We placed 30 mist nets (12 m x 3 m with 36 mm mesh) in the three major habitat types that vary by proximity to water and forest age (Table 1 and Figure 1). Nets in upland TMF were generally relatively distant from permanent water and were in mature primary forest, except for areas of secondary growth recovering from landslides such as the area of habitat damage indicated in Figure 1. Nets in Riparian Secondary Growth TMF were in the lower part of the Nambillo River valley in forest that had been regenerating from pasture for ~25 years. All nets in Riparian Secondary Growth TMF were within 130 m of the Nambillo River. Nets in the Ecotone Habitat varied in proximity to water and density of understory vegetation and were distributed at the edges of remnant TMF throughout the fragmented landscape mosaic (Figure 1).

Each year for six years (2013-2018) we netted birds in the three habitat types during the first two weeks of December. We typically operated nets for five hours in the mornings (~0600–1100) on two consecutive days each in the Mature Upland TMF and Riparian Secondary Growth TMF sites. We netted for three consecutive days in the Ecotone Habitat because capture rates were higher. With 30 nets in each habitat, this yielded 300 net-hours (nh) in each of the Mature Upland TMF and Riparian Secondary Growth TMF habitats and 450 nh in the Ecotone Habitat per year. Due to unstable slopes and habitat damage, we did not operate nets in the Mature Upland TMF in 2017, and instead completed an additional 150 nh in the Riparian Secondary Growth TMF. Nets were spaced 0-60 m apart on small paths in each habitat. We recorded the usual morphometric data as follows for each bird captured, including resident and migratory birds: species, sex, age, weight (g), unflattened wing chord (mm), exposed culmen (mm), tail length (mm), and tarsus (mm). We also noted body and furculum fat, molt in primary feathers, tail, and body feathers, reproductive state (primarily for resident birds), and types of ecto-parasites. Data that was collected but not discussed here is to be used in future publications. Swainson's Thrushes with wing chord measurements of 100 mm or larger were determined to be males, those with wing chord measurements of 93 mm or smaller were determined to be female, and those with measurements between 93 mm and 100 mm were noted as unknown (Covino 2015).

Statistical analyses were completed in JMP 8.0.2 (SAS 2009) with *alpha* set at 0.05, and with ANOVA means and standard errors presented. Variation is not repeated on graphs.

RESULTS

During 6,150 net-hours of total effort, we netted 96 Swainson's Thrush individuals in 108 capture events. Ages at first capture were 61.5% After Hatching Year (AHY), 36.5% Hatching Year (HY), and 2% (two individuals) unknown that could not be aged accurately (U). We determined the sex to be male in 32 individuals, female in six individuals, and unknown in 58 individuals. Of the 96 individuals, six were caught in multiple years. This included one that was initially caught as an AHY while the other five were caught as HY and were recaptured returning to the site as AHY in subsequent years. We determined one to be a female, two as males, and three as unknowns (Table 2). The distances between initial captures and recaptures in subsequent years ranged from 0 m (same net) to 63 m, with one male that was captured and recaptured within 27 m of the initial capture net during four different winters (Table 2).

We also re-captured four individuals within the same year as initial capture, although none of these captures were more than 1 day apart. These were all males and they included two AHY birds, one HY, and one was an AHY that had been caught

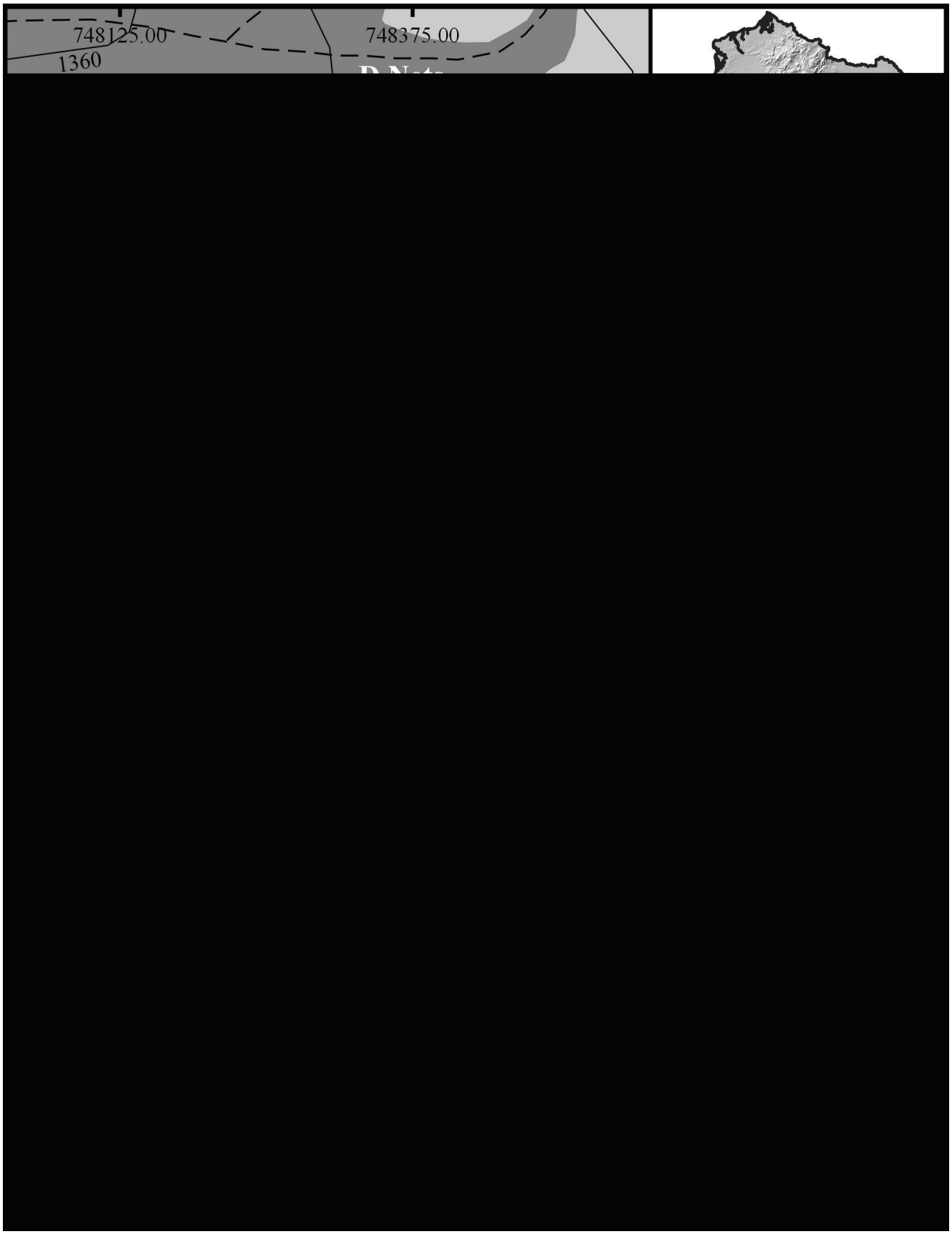

Figure 1: Map of the study area showing net locations, elevation contours, water features, and major habitat types

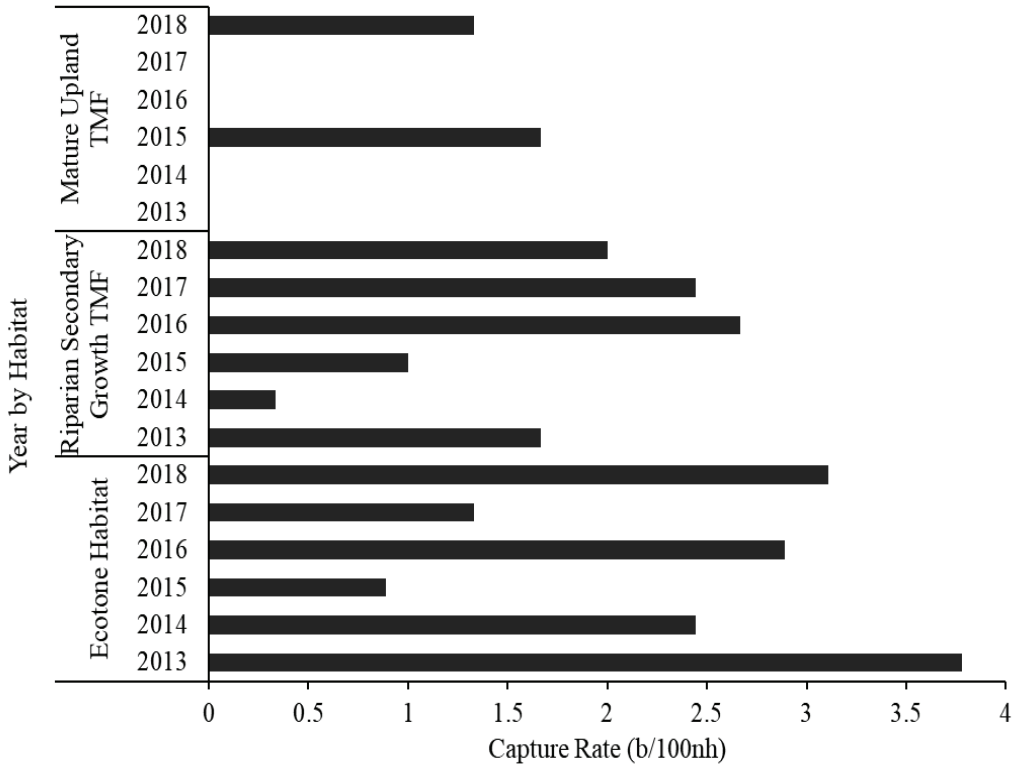

Figure 2: Swainson's Thrush capture rates (birds per 100 net-hours) by year within each habitat. Note: Capture rates in 2013, 2014, and 2016 in the Mature Upland TMF habitat were truly 0 while we did not net there in 2017.

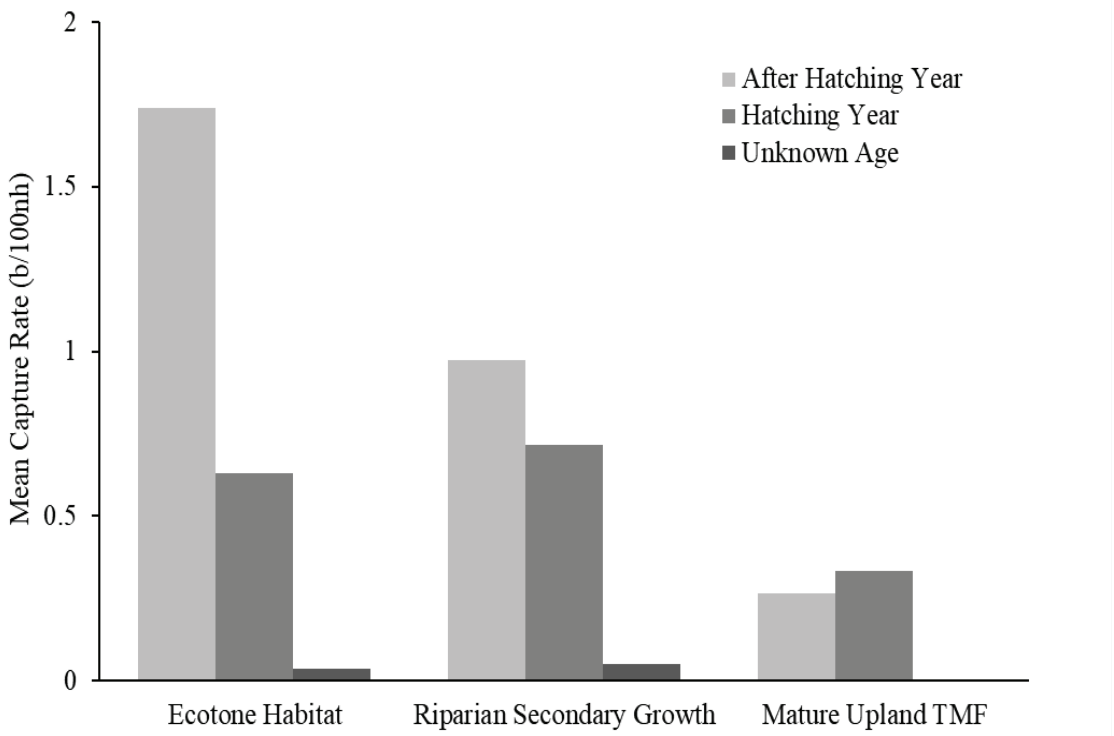

Figure 3: Swainson's Thrush mean capture rates (birds per 100 net-hours) by age in each of the three habitats, averaged across all years from 2013-2018.

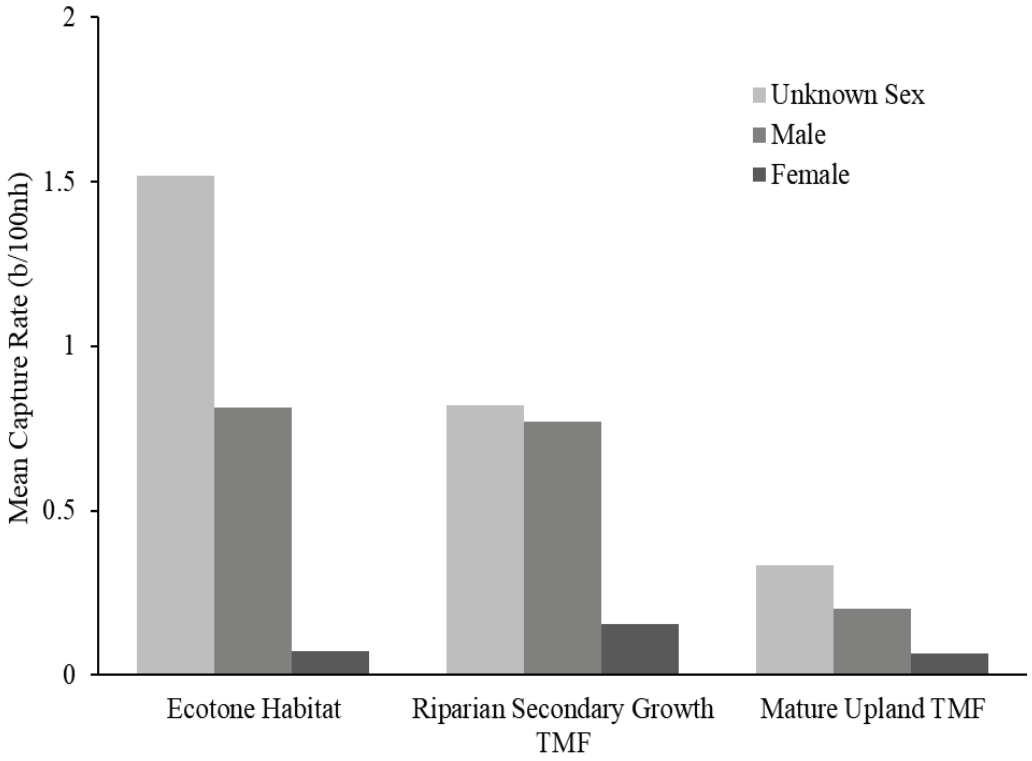

Figure 4: Swainson's Thrush mean capture rates (birds per 100 net-hours) by sex as determined by wing chord measurements in each of the three habitats, averaged across all years from 2013-2018.

Table 1. Mist net sites, habitat variables, and netting effort at Reserva Las Tangaras, Ecuador, Decembers 2013-2018 (TMF = tropical montane forest).

Habitat	Elevation Range (m)	Distance to water feature (m)	Age of forest (yr)	Total Net-Hours
Mature Upland TMF	1320–1520	70–285	>200	1500
Riparian Secondary Growth TMF	1300–1380	<130	25-30	1950
Ecotone Habitat	1300–1440	3–65	2-7 (Abandoned Pasture) >200 (Remnant TMF)	2700

Table 2. Swainson's Thrush annual return recovery data at Reserva Las Tangaras, Ecuador 2013-2018, net locations, and estimated number of round-trip migrations. B & C nets were in the Ecotone Habitat, primarily along drainages and S & R nets were in the Riparian Secondary Growth TMF, as indicated in Figure 1.

Band Number	Sex	Age when Banded	Year Banded	Recovery Years	Nets by Capture Year (See Figure 1)	Max Distance between Captures (m)	Number of Migrations
1531-59116	U	HY	2013	2014	D4, D5	19	1.5
1531-59120	M	HY	2013	2014, 2016, 2018	B8, B7, B7, B6	27	5.5
1531-59121	U	HY	2013	2014	B5, B6	12	1.5
1531-59147	M	AHY	2015	2018	S8, S3	40	3.5
1531-59150	F	HY	2016	2017	R2, R2	0	1.5
1531-59157	U	HY	2017	2018	C4, C2	63	1.5

Table 3. Swainson's Thrush same year recovery data at Reserva Las Tangaras, Ecuador 2013-2018 and net locations. B & C nets were in the Ecotone Habitat, primarily along drainages and S & R nets were in Riparian Secondary Growth TMF, as indicated in Figure 1.

Band Number	Sex	Age when Banded	Initial Capture Date	Same Year Recovery Date	Nets by Capture (Figure 1)	Distance between captures (m)
1421-00435	M	HY	12/07/2017	12/08/2017	R4, R1	79
1421-00440	M	AHY	12/12/2017	12/13/2017	B1, B5	76
1421-00450	M	AHY	12/13/2018	12/13/2018	C5, D2	235
1531-59147	M	AHY	12/06/2018	12/07/2018	S3, S3	0

initially as an AHY in a previous year and was re-captured twice within a subsequent year (Table 3). The distances between initial and subsequent captures within the same year ranged from 0 m to 235 m (Table 3).

Annual capture rates of the thrushes (birds per 100 net-hours) varied significantly by habitat type (ANOVA, df $F_{2,14}$ = 4.89, P = 0.0244) (Figure 2). Mean capture rate was highest in the Ecotone Habitat (2.4 ± 0.37 b/100nh [N = 6]), intermediate in Riparian Secondary Growth TMF (1.68 ± 0.39 b/100nh [N = 6]), and lowest in Mature Upland TMF (0.6 ± 0.43 b/100nh [N = 5]) where there were 0 captures in 3 out of 5 years, excluding 2017 when we did not band in the Mature Upland TMF. Only the mean capture rates in the Ecotone Habitat and Mature Upland TMF were significantly different (Tukey-Karmer HSD, P = 0.019). There was no significant year effect on capture rates.

Capture rates of AHY thrushes (Figure 3) had a pattern similar to that of the total capture rates and also varied significantly by habitat (ANOVA, df $F_{2,14}$ = 5.67, P > F = 0.016) with the highest mean rate in the Ecotone Habitat (1.74 ± 0.29 b/100nh), an intermediate mean rate in Riparian Secondary Growth TMF (1.01 ± 0.29 b/100nh), and the lowest mean rate in Mature Upland TMF (0.26 ± 0.32 b/100nh). Again, only capture rates of AHY birds in the Ecotone Habitat and Mature

Upland TMF were significantly different (Tukey-Karmer HSD, P = 0.012). Capture rates of HY birds showed no significant difference by habitat, although the mean rate in Mature Upland TMF (0.33 ± 0.25 b/100nh) was half the rates associated with the Ecotone Habitat and Riparian Secondary Growth TMF, 0.63 ± 0.23 and 0.61± 0.22 b/100nh, respectively.

We only evaluated variation in habitat of capture for males as there were not enough data to statistically evaluate variation for females (Figure 4). There was no statistically significant difference in male capture rates by habitat, but again the pattern was similar to total captures with the Ecotone Habitat and Riparian Secondary Growth TMF mean capture rates, 0.81 ± 0.19 and 0.76 ± 0.19 b/100nh, respectively, being nearly quadruple those in the Mature Upland TMF (0.20 ± 0.21 b/100nh).

DISCUSSION

Several Swainson's Thrush individuals showed remarkable annual site fidelity, returning to generally the same net locations in multiple years with some recoveries occurring in the exact same net as the original capture (Table 2). One male Swainson's Thrush appears to have made the round-trip migration between Ecuador and North America five times and was captured most recently during its 6th winter at the study site in December 2018 (Table 2). It is interesting to note that five of the six annual returning individuals were initially caught as HY birds.

Although six individuals returned to our study area over multiple years and four individuals were recaptured in the area during a single year, we lacked multiple sessions within a single winter to be able to assess overwintering site persistence. While we are not certain that the thrushes we recover stay in our study area for the entire winter period, their consistent returns somewhat challenge earlier claims that Swainson's Thrushes are nomadic during the winter (Rappole and Warner 1980). More intensive netting involving multiple sessions per winter and additional nets could resolve the uncertainty regarding overwintering persistence and the magnitude of the annual return rate.

Swainson's Thrushes at Reserva Las Tangaras had highest capture rates in the Ecotone Habitat and in Riparian Secondary Growth TMF near the Nambillo River. Capture rates in Mature Upland TMF were comparatively low, suggesting that wintering Swainson's Thrushes prefer habitats with water features independent of forest maturity and fragmentation. These results for a wintering site are similar to those noted for breeding grounds, where Swainson's Thrushes also prefer ecotones with water features and dense understory (Timossi 1990) as well as riparian over upland habitats (Darveau et al. 1995).

Our significantly greater capture rates for AHY birds in the Ecotone Habitat versus Mature Upland TMF, lack of difference in HY bird capture rates between habitats, and the comparatively low capture rates of HY birds in habitats preferred by AHY thrushes may indicate that younger birds have a subordinate status and must use less favorable habitats (Gauthreaux 1978). It is also possible that HY thrushes become more selective of particular habitats as they age and gain experience with habitat variation as found in some other passerines. Young Wilson's Warblers (*Cardellina pusilla*) were similarly more prevalent in less favorable habitats at migratory stopover sites compared to adults (Yong et al. 1998). In contrast, Bicknell's Thrushes (*Catharus bicknelli*) show no variation in age ratios by winter habitat characteristics (Townsend et al. 2011).

We did not find a significant difference in capture rates by sex in our three habitat types, but overlap in wing chord shown by male and female thrushes resulted in the majority of thrushes in our study categorized as unknown sex. We must also acknowledge that our habitat classifications were very broad.

Given the apparent annual site fidelity of wintering Swainson's Thrushes at the Reserva Las Tangaras study site, light-level geolocators could be employed to determine where these birds breed, how long they stay in our study area, and their migratory routes (Cormier et al. 2013, Delmore et al. 2012). While most tracking of migrants is done from breeding grounds, a reverse approach seems feasible from Reserva Las Tangaras. Additional mist netting sessions in winter may increase the

likelihood of recoveries and resolve the uncertainty regarding overwintering site persistence. By discovering migratory routes, future studies could characterize the habitats at migratory stopover sites to determine additional areas to focus conservation efforts.

Finally, because Swainson's Thrushes were more prevalent in riparian habitats during our winter monitoring, we conclude that clearing riparian vegetation for recreation or cattle grazing, as is commonly done in Ecuador, will have negative impacts on this species. Conservation efforts for these thrushes must continue in both South and North America with a strong focus on protecting both breeding and wintering riparian habitats.

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